

Patterns and Consequences of Whole Colony Growth in the Compound Ascidian *Polyclinum planum*

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Abstract. The size and shape of colony-forming modular animals can convey ecological advantages, but many patterns and consequences of colony-level growth are not well understood. I carried out a longitudinal study on an intertidal population of the pedunculate ascidian *Polyclinum planum* to determine the patterns and consequences of its colony growth. I found that each *P. planum* colony is a nonfragmenting genet, and that colony size is limited by water-flow forces and reproductive state. *P. planum* mitigates the effects of water-flow forces by having an attenuating pattern of growth and by producing a laterally flattened, zooid-bearing lobe atop its tough flexible peduncle. Growth slows as the colony nears a size limit set by the environment and as it becomes reproductively active. The laterally flattened lobe allows colonies to increase their surface-to-volume ratio, to house increased numbers of zooids (thereby increasing reproductive potential), and to minimize the effects of the acceleration reaction of water. *P. planum*'s growth pattern fits predictions for colonies living in wave- or surge-impacted environments. The growth of *P. planum* provides insight into how indeterminate modular growth conveys ecological and reproductive advantage, even amidst a physically stressful environment.

Introduction

Theories describing the indeterminate growth of colony-forming modular organisms suggest that the colonies have the potential to grow linearly or exponentially throughout their postlarval lives (Jackson, 1977; Sebens, 1987). Sebens (1987) defines three patterns of indeterminate growth, two of which (Indeterminate Growth Types

II and III from his paper) are applicable to colony-forming modular organisms. In Sebens' (1987) Indeterminate Growth Type II (Plastic Exponential Growth), energy intake and expenditures occur at the level of each member (module) of a colony, thus allowing each module to contribute independently to the colony and producing continuous linear or exponential growth—a growth pattern reported by Hughes and Jackson (1985) for stony corals, by Karlson (1988) for a zoanthid, by Pätzold *et al.* (1987) for a bryozoan, and by Bak *et al.* (1981) for a compound ascidian. In Sebens' (1987) Indeterminate Growth Type III (Plastic Attenuating Growth), colony growth rates decrease as colony size increases, growth being limited largely by environmental factors before internal energetic constraints take effect—a growth pattern reported by Hughes and Connell (1987) for stony corals, by Karlson (1988) for a zoanthid, and by Denny *et al.* (1985) for a hydrocoral.

External factors therefore constrain growth in some situations, but internal constraints are also known to be limiting in some taxa. For example, Millar (1952, 1971) and Bak *et al.* (1981) report that ascidian colonies grow rapidly when they are not reproductive, but that growth slows or ceases during reproduction. For at least some modular species, colony growth and reproduction are physiologically incompatible processes.

To evaluate the applicability of growth predictions for a colony-forming modular organism, one must understand how environmental effects (external factors) and life-history constraints (internal factors) affect colony growth. It is, unfortunately, difficult to collect those kinds of life-history data for many colony-forming modular species. The difficulty arises because there is often no way of knowing whether a colony encountered in the field developed directly from a larva or was one of many ramets produced by fragmentation (for examples, see Hughes, 1984; Hughes and Jackson, 1985; Karlson,

Received 24 July 1995; accepted 24 October 1996.

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1986, 1988; Rosen, 1986; Lasker, 1990; McFadden, 1991; Stocker, 1991). That uncertainty eliminates the possibility of measuring age-related effects at the level of genets. To further complicate matters, ramets of some modular species can fuse with other ramets of the same or different genotype (Hughes and Jackson, 1985; Rinkevich and Weissman, 1987a, b; Stocker, 1991; Pancer *et al.*, 1995). One way to be sure of the origins, ages, and fates of colonies of modular organisms is to conduct longitudinal site surveys, as suggested by Berrill (1950) when he stated that "the age of (compound) ascidians is practically impossible to estimate, unless a certain inhabited area is followed closely through seasons and years." That is sound advice if one hopes to understand the life histories of modular species, because age, size, and shape of modular colonies may not be as tightly linked as those parameters are to body size among unitary organisms (Hughes and Jackson, 1980; Jackson and Coates, 1986; Hughes and Connell, 1987).

In the present study I use monthly site surveys conducted over 2.5 years to describe the pattern of whole colony growth and the consequences of that growth for intertidal *Polyclinum planum* growing *in situ*. In so doing I try to determine whether the growth pattern of *P. planum* colonies more closely approximates Sebens' (1987) Type II or III pattern of growth, or some other pattern, and to discern what factor or factors constrain whole colony growth in this species.

I hypothesize that the growth pattern of *P. planum* will be more similar to Sebens' (1987) Growth Type III (Plastic attenuating growth) than to his Growth Type II (Plastic exponential growth). I chose Type III rather than Type II because the colonies at my study sites live in a wave- and surge-impacted environment, and the associated water-flow forces may impose limits to colony size.

Water-flow forces present an obvious ecological risk to erect, though flexible, intertidal *P. planum* colonies. Denny *et al.* (1985) demonstrated how the water-flow forces of drag, lift, and, most importantly, acceleration can dislodge or limit the size of intertidal organisms. Because the *P. planum* colonies at my sites are constantly subjected to water-flow forces, they should have adaptations for dealing with those forces that will be evidenced as the colonies increase in size.

I also hypothesize that the onset of reproduction in *P. planum* colonies will limit growth, and that large colonies will show more evidence of reproductive activity than small colonies. A *P. planum* colony grows by strobilation of its zooids. Strobilation, however, precludes gonadogenesis and larval brooding by the zooid because gonads develop only in its post-abdomen and larvae are brooded only in its atrial chamber—structures that become disorganized during strobilation (Holyoak, 1992).

P. planum, an aplousobranch ascidian, is well suited

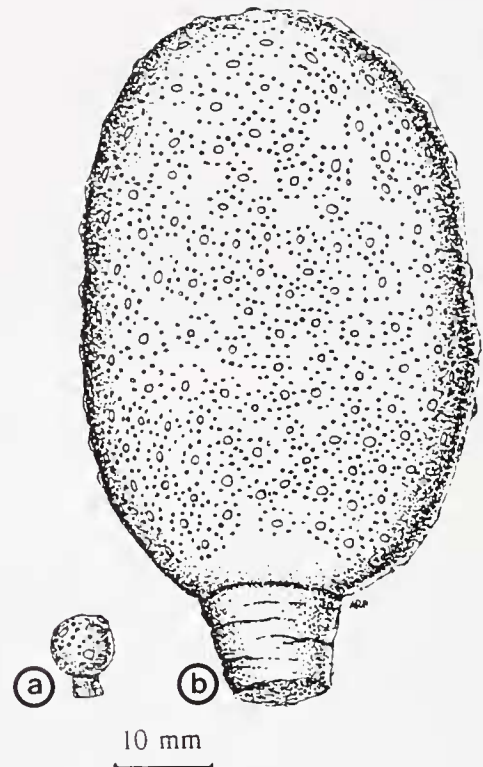


Figure 1. (a) Small "recruit-sized" *Polyclinum planum* colony with a spheroidal zooid-bearing lobe atop its zooid-free peduncle. (b) Large *P. planum* colony with a laterally flattened lobe. Note: Silhouette shapes of larger colonies are highly variable.

to a longitudinal investigation of colonial growth. It has a distinctive colony form—a fleshy, zooid-bearing lobe supported by a tough and flexible peduncle—that makes it readily identifiable in the field even when colonies are small (Fig. 1). *P. planum* colonies are not believed to fragment, so a single colony represents an entire genet (Pearse *et al.*, 1989). The nonfragmenting growth of these colonies eliminates the confounding effects of not knowing whether a colony is a ramet or an unfragmented genet. The loss of a *P. planum* colony is consequently a greater loss to the population, from an evolutionary perspective, than the loss of one ramet from a population of fragmenting genets. Since a genet of *P. planum* does not spread its genes across several physiologically isolated ramets, one would expect this species to display strategies that allow individual colonies to minimize ecological risks and to maximize reproductive productivity.

Materials and Methods

Between December 1989 and May 1992, I monitored the whole colony growth of intertidal *Polyclinum planum* *in situ* at the Hopkins Marine Station (HMS), Pacific Grove, California. The colonies there live attached

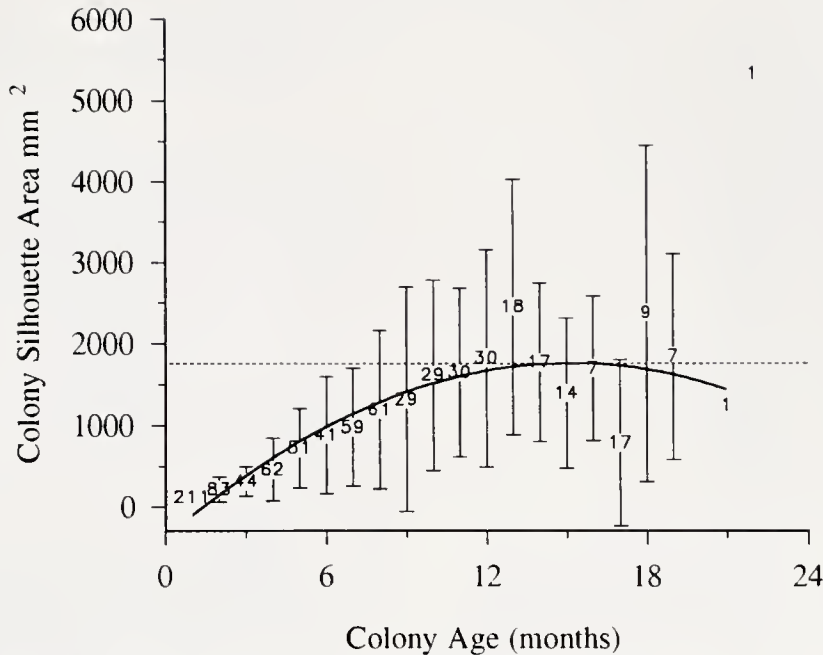


Figure 2. Mean growth trajectory of *Polyclinum planum*. A quadratic regression provides a significant fit to the data ($Y = -377.06 + 283.09x - 9.38x^2$; $r^2 = 0.734$; $t = -3.59$; $df = 17$; $P < 0.005$). Numbers indicate the number of observations included in each age class, error bars are standard deviations, and the horizontal dashed line indicates the maximum size (colony-silhouette area in mm^2) of the growth trajectory. The single outlier at month 23 was not included in the curve-fitting analysis. Discrepancies between numbers of colonies indicated for each age class (month) on this figure compared to Figure 7 are due to the fact that I was typically able to map all colonies at my sites each month, even with marginal tide conditions, but I was not able to photograph all colonies in months with marginal tides.

to granitic substrates below about -0.3 m MLLW (Mean Lower Low Water tide) and are most abundant in areas where granitic outcrops covered by surfgrass (*Phyllospadix* sp.) are protected from direct wave action. The highest density of *P. planum* I encountered during preliminary surveys prior to establishing my study sites was 95 colonies in a single 0.25-m^2 quadrat, though the mean of 7.8 colonies per 0.25-m^2 quadrat ($SD = 14.95$ colonies; $n = 45$ 0.25-m^2 quadrats surveyed in the intertidal zone at HMS) was more representative of *P. planum* densities at HMS.

I established three study sites, each about 1 m^2 , at -0.3 m MLLW; all had *P. planum* colonies present at the beginning of the study. The sites were within 10 m of each other and all of them had a dense canopy of surfgrass covering a mosaic of encrusting organisms, foliose algae, and bare rock surfaces. The three sites were on the inshore side of massive granitic outcroppings along the outermost reaches of the HMS intertidal zone. Most of the force produced by waves was typically expended on those rocks. *P. planum* colonies were nevertheless subjected to surge conditions as water from breaking waves flowed over and around the outcroppings during all but the lowest tides. Because *P. planum* lives low in the in-

tertidal zone, my study sites were accessible for only hours at a time and only in months with sufficiently low tides. This somewhat limited access occasionally hampered data collection. For this paper describing patterns of colony growth, data from the three sites were pooled.

Three lag bolts were anchored at each site and used to locate the sites and to aid in mapping the locations of all *P. planum* colonies. A colony's position was mapped monthly by measuring the distance between its peduncular point of attachment and the three lag bolts. A mapped colony was then manipulated gently so that the full silhouette view of its zooid-bearing lobe (along with a 15-cm ruler, for scale) could be photographed. Colonies thus censused could thereafter be identified by their map coordinates and photorecords. Colonies that appeared on the study sites for the first time and were large enough to be positively identified as *P. planum* (with a lobe-silhouette area typically between 50 and 200 mm^2) were referred to as "recruits." A colony's post-recruitment life span ended when it was dislodged from its mapped location.

Photographs of colonies were digitized, and the silhouette areas of zooid-bearing lobes were measured by means of video imagery analysis (Image version 1.43).

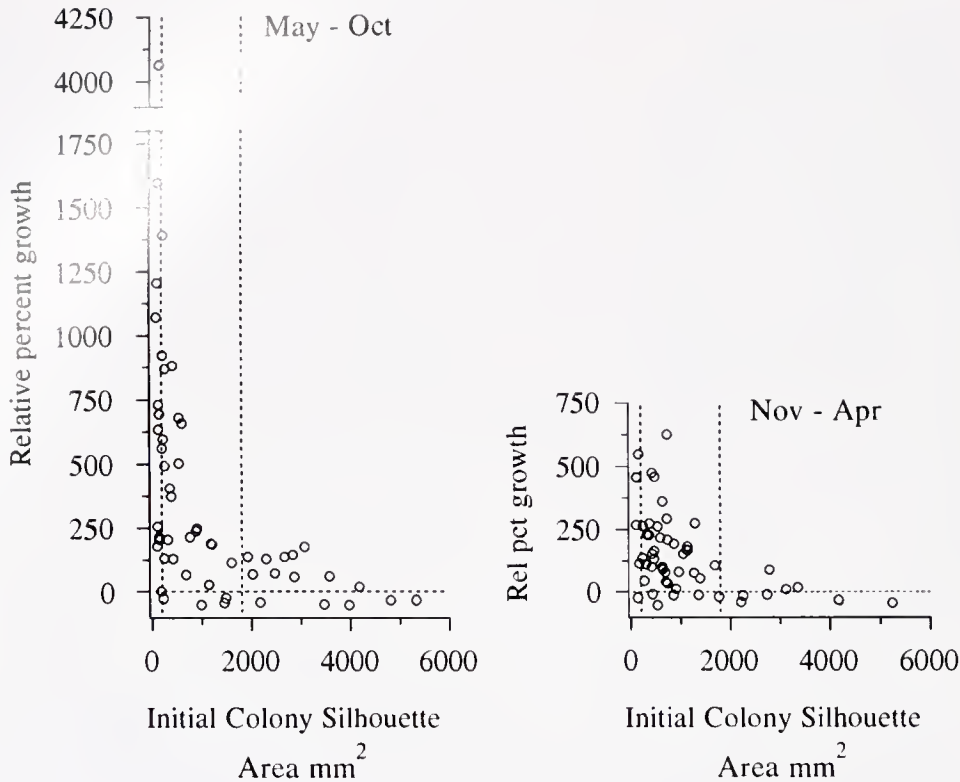


Figure 3. Relative percent growth of *Polyclinum planum* colonies by size and season. The graph on the left shows growth of 55 colonies during calm, warm-water months; the graph on the right shows growth of 53 colonies during months with colder, rough sea-state conditions. Vertical dashed lines delineate colony size classes (small = <200 mm² lobe-silhouette area; medium = 200–1800 mm²; large = >1800 mm²).

Lobe silhouette areas were used to generate a mean growth trajectory for *P. planum*. I used stepwise polynomial regression (Zar, 1984) as a descriptive tool to fit a curve to the mean growth data. That curve should not be used to make statistical comparisons, however, because the monthly data included individual colonies that were sampled multiple times (*i.e.*, in consecutive months), and therefore violate the assumptions of independence required for regression analysis. Consequently, comparisons of *P. planum*'s mean growth trajectory to theoretical growth curves are unavoidably qualitative.

To determine where new material (zooids and tunic) is added to zooid-bearing lobes of growing colonies, I manipulated eight of the colonies on my sites. I tied loops of cotton-wrapped nylon thread through three points on their lobes—one loop through the lobe near the peduncle, one loop through the center of the lobe, and one loop through the lobe near the lobe tip. In successive months I measured distances between those marks, and between the marks and lobe edges.

In April 1991 I began measuring the thickness of lobes and calculating a lobe flatness value for each colony by dividing a lobe's maximum width by its maximum thick-

ness. Spheroidal lobes had flatness values of 1.0, and colonies with lobes wider than they were thick had flatness values greater than 1.0. Those values were used to generate a mean trajectory of lobe flattening for *P. planum*. I again used stepwise polynomial regression to fit a curve to the trajectory of lobe flattening.

At the end of my study, in May 1992, I collected 77 *P. planum* colonies from the study sites to test for relationships between colony age, size, and reproductive state. Those colonies ranged from 66 mm² to 5661 mm² in size (colony-silhouette area) and from 1 to 24 months in age.

I determined the reproductive state of those colonies by cutting three wedge-shaped pieces from the lobe of each colony—one from the lobe tip and one from each lateral edge of the colony. I counted the total number of exposed zooids on one side of each wedge, the number of those zooids undergoing strobilation, and the total number of larvae brooded by the nonstrobilating zooids. I also dissected the post-abdomen from four nonstrobilating zooids per wedge and measured the largest oocyte from each one. I used chi-square analyses to test for effects of colony age and colony size on reproductive

condition of *P. planum*. I also used linear regression to test for the effect of colony age on colony size.

Results

Polyclinum planum colonies were present on the research sites throughout the study. Recruitment and dislodgement of colonies occurred year-round, as did colony growth. The colonies did not fragment: each recruit produced only one pedunculate colony. During the study 211 *P. planum* colonies appeared at the study sites as recruits and became dislodged between 1 and 23 months later. The mean value for maximum lobe-silhouette area attained by those colonies was 803.0 mm² (SD = 1224.4 mm²; $n = 211$ colonies). The largest of those colonies had a lobe-silhouette area of 8511 mm² at 17 months of age.

The mean post-recruitment life span of *P. planum* was 5.52 months (SD = 5.49 months; $n = 211$ colonies). The longest-lived colony on my sites persisted an exceptional 24 months. That colony did not become dislodged during the course of this study, so it was not used in analyses that included data only from colonies that did become dislodged.

Mean growth trajectory

Mean colony size was plotted against age in months to generate a growth trajectory for *P. planum* (Fig. 2). The mean growth trajectory included a period of rapid growth throughout the first 10–12 months, followed by a period of attenuating growth to a mean maximum size of 1759 mm² at month 15. The growth trajectory also indicated a decline in colony size among older colonies. Most colonies aged 14 months or older (21 of 27 colonies = 77.8%) decreased in lobe-silhouette area before being dislodged. The 21 colonies that experienced a size decrease lost an average of 42.4% (SD = 25.5%) of their maximum lobe-silhouette area prior to dislodgement. Some colonies decreased in size gradually, by abrasion; others lost larger pieces of their lobes, presumably in a single event, the explanation of which remains problematic.

The growth data also revealed increasing size variability within age classes throughout the first 9 months. After the 9th month standard deviations were so wide in some age classes that they overlapped the mean values of virtually all other age classes (for example, see Fig. 2, months 9, 12, 13, and 18). This trend suggests that colony age and size were not as tightly linked among larger colonies as among smaller ones, thus demonstrating the indeterminate nature of *P. planum* colony growth.

Relative percent growth of *P. planum* colonies, comparing colony-silhouette area at the beginning and end of 6-month intervals—May through October (months with

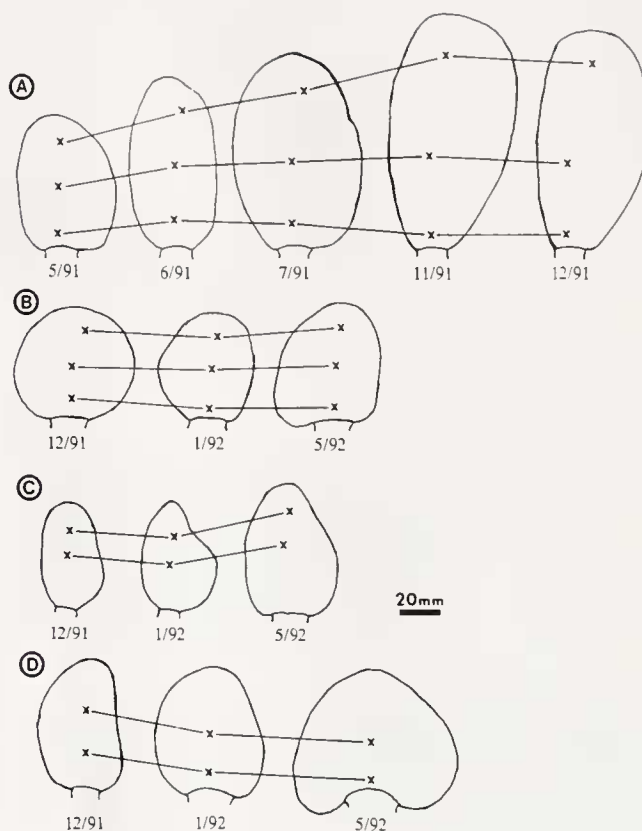


Figure 4. Patterns of lobe expansion for four colonies with marked lobes. An "X" indicates the location where a loop of thread was tied through the zooid-bearing lobe.

calmer sea-state conditions) or November through April (months with rougher sea-state conditions)—confirmed the general trends of size-specific growth indicated by the mean growth trajectory. Smaller colonies grew more rapidly than larger colonies (Fig. 3). Those growth data also suggest a seasonal effect on growth rates: the smallest size class of colonies exhibited much greater increases in relative percent growth during periods of calmer and warmer sea-state conditions (between May and October) than did colonies of similar initial size during rougher and cooler sea-state conditions (between November and April).

To test for seasonal effects on size-specific relative percent growth, I assigned colonies to three size classes: (1) small (<200 mm² colony-silhouette area; the size of most recruits); (2) medium (200–1800 mm²; colonies larger than recruits but smaller than the maximum size indicated by the growth trajectory); and (3) large (>1800 mm²; colonies larger than the maximum colony area indicated by the growth trajectory). *T*-tests showed a significant seasonal effect on growth of medium-sized colonies ($t = 3.309$; $df = 65$; $P = 0.0014$). There was no seasonal effect on growth of large colonies ($t = 1.874$; df

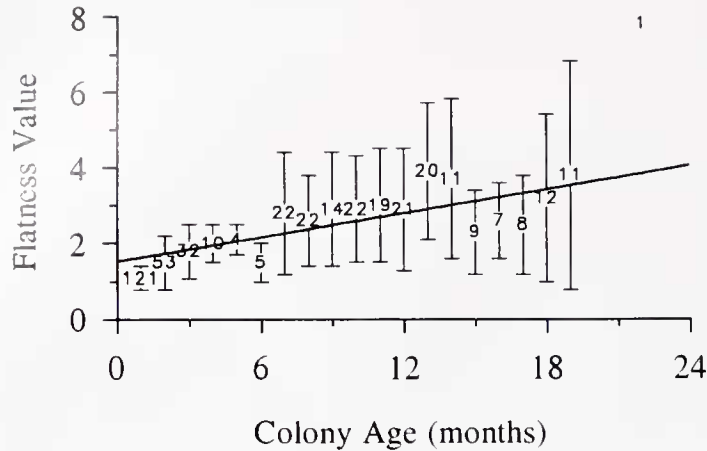


Figure 5. Mean trajectory of lobe flattening for *Polychnum planum*. A linear regression provides a significant fit to the data ($Y = 1.528 + 0.106x$; $r^2 = 0.568$; $t = 4.73$; $df = 17$; $P < 0.001$). Error bars are standard deviations, and numbers indicate the number of observations included in each age class. The single outlier at month 23 was not included in the curve-fitting analysis. The numbers of colonies indicated per month on this figure differ from those of Figure 2 because I began measuring lobe thicknesses in April 1991, and I began measuring lobe silhouette areas (shown in Fig. 2) in December 1989.

= 22; $P = 0.074$) or small colonies ($t = 1.246$; $df = 15$; $P = 0.232$). The lack of a seasonal effect on small colonies is probably due to the extremely wide variability of growth displayed by small colonies in the May–October group (Fig. 3).

Intra-colony growth

Four of eight colonies with marked lobes persisted long enough to show where *P. planum* can add new material to the zooid-bearing lobe (Fig. 4). Colony A added new material in a diffuse manner throughout the length and width of its lobe. More material was added between the middle mark and the mark furthest from the peduncle than between the middle and proximal marks. After July 1991, colony A also added more material along its right side than along its left side. Colony B decreased slightly in size in January 1991, after which material was added to the left side of the colony. Colony C added more material to the lobe proximal to the peduncle than distally, causing the two marked spots on this colony to move away from the peduncle but not much farther from each other. Colony C also added material along the left and right sides of the lobe. Colony D added material along the right and left sides of its lobe, producing a spade-shaped silhouette. The peduncle of that colony also expanded upward into the lobe, causing the marked spots to appear to move closer to the peduncle.

Mean trajectory of lobe flattening

Zooid-bearing lobes of small colonies changed gradually from a spheroidal shape to a laterally flattened discoidal shape as they grew (Fig. 5), becoming what were

essentially bilayered sheets of zooids. Lobes of recruits had a mean cross-sectional flatness value of 1.1 (SD = 0.3; $n = 121$ recruits appearing between April 1991 and May 1992). The flattest colony measured was 20 months old; it had a lobe width of 113.5 mm and a flatness value of 12.6. Stepwise polynomial regression showed that a linear function best described changes in colony flatness. The mean flatness value of the regression was 2.53. The linear function of the regression shows that ratios of lobe width to thickness typically increase throughout a colony's life span. Increases in lobe-flatness values are largely the result of the expansion of lobe width, because lobe thickness typically did not decrease during a colony's life span.

Recruitment and survivorship

Simple (least squares) linear regression showed that the number of *P. planum* recruits appearing at the study sites each month was not significantly dependent upon surface water temperatures (Fig. 6; $r^2 = 1.46 \times 10^{-6}$; $df = 1,21$; $P > 0.75$) (seawater temperatures were measured daily by HMS staff). Likewise, the number of recruits appearing monthly at the study sites was not dependent upon the number of days of strong surge conditions per month ($r^2 = 0.022$; $df = 1,21$; $P = 0.5$). Seawater temperature and surge conditions were measured by HMS staff. Linear regression of the number of colonies dislodged per month on water temperature did, however, indicate a significant relationship ($r^2 = 0.345$; $df = 1,21$; $P < 0.005$), as did the regression of the number of colonies dislodged per month on the number of days of strong surge per month ($r^2 = 0.256$; $df = 1,21$; $P < 0.025$).

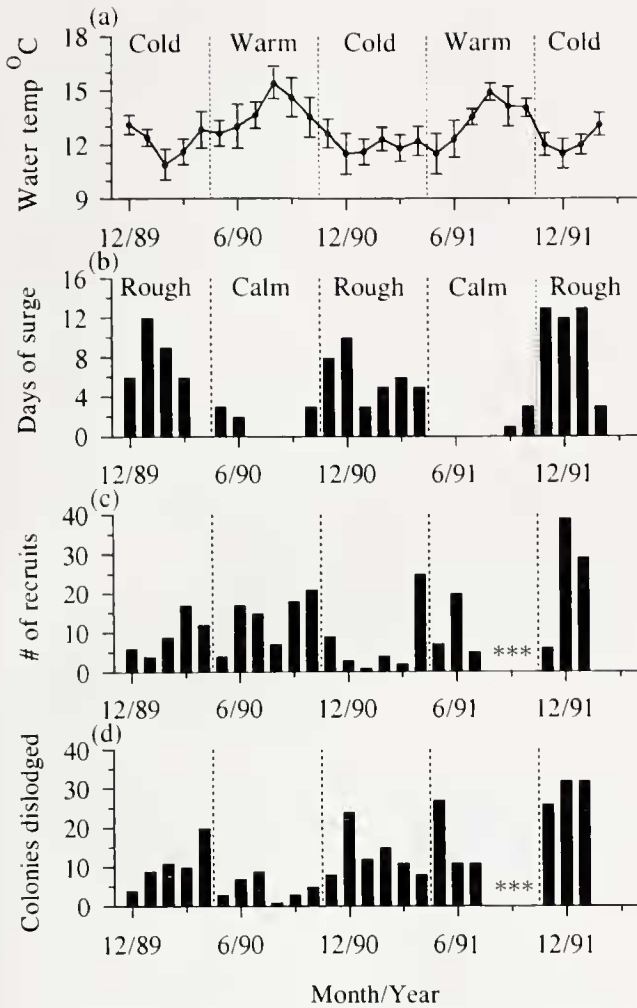


Figure 6. (a) Mean monthly surface seawater temperature at Hopkins Marine Station (HMS); (b) number of days of strong surge conditions per month at HMS; (c) number of recruits appearing at the research sites per month; (d) and number of colonies dislodged from research sites per month. Vertical dashed lines indicate break points between warm months with calm sea-state conditions and colder water months with rougher sea-state conditions. Asterisks on the two lower graphs indicate months during which data could not be collected. Data on seawater temperature and sea-state condition were collected by and provided courtesy of HMS staff.

Significantly more colonies were dislodged from the study sites during months with rough (as defined by HMS staff) sea-state conditions (Nov–Apr; \bar{x} = 7.2 days of strong surge per month; SD = 3.7 days) than during months with calmer sea-state conditions (May–Oct; \bar{x} = 1.0 day of strong surge per month; SD = 1.3 days), as indicated in Table 1.

For both small and large colonies, the proportion of colonies dislodged was significantly larger during rough months than during calm months (Table 1). There was, however, no statistical difference between the proportion

Table 1

The number of *Polyclinum planum* colonies dislodged per size class by season

	Colony size class (colony-silhouette area in mm ²)		
	0–200	200–1800	>1800
Strong surge (Nov–Apr)	75 (62.5)	74 (69.9)	44 (31.4)
Calm (May–Oct)	21 (33.5)	39 (43.1)	13 (25.6)
Column χ^2 values	7.16*	0.63 NS	11.26***
Contingency table χ^2 value = 19.05***			

The results of a chi-square analysis of this 2 × 3 contingency table and the results of chi-square tests for each column are indicated. Numbers in parentheses are the expected values for each cell.

* = $P < 0.01$; *** = $P < 0.001$; NS = not significant.

of medium-sized colonies dislodged in rough versus calm months. The medium-sized colonies had survived early post-recruitment mortality but had not grown large enough to exceed the maximum colony size of the mean growth trajectory.

Age- and size-dependent survivorship data (Fig. 7) showed that the greatest mortality occurred among the youngest colonies (39.3%—83 of 211 colonies) and among the smallest colonies (47.9%—101 of 211 colo-

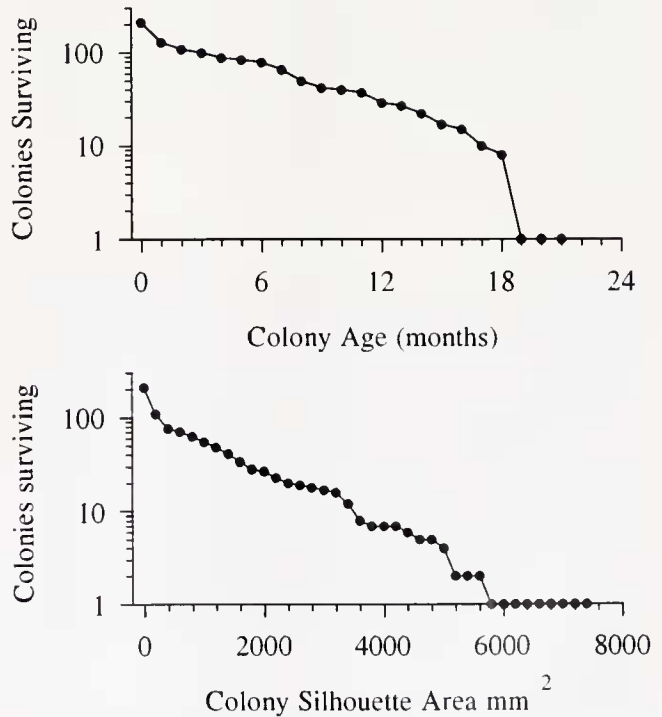


Figure 7. Age-dependent and size-dependent survivorship curves for *Polyclinum planum*.

Table II

Comparisons of number of colonies in each size class with zooids undergoing strobilation, bearing oocytes, and brooding larvae

	Colony size classes (colony silhouette area in mm ²)		
	0-200	200-1800	>1800
Strobilation			
100% zooid strobilation	11 (5.45)	23 (23.64)	1 (5.91)
<100% zooid strobilation	1 (6.55)	29 (28.36)	12 (7.09)
Column χ^2 values	10.35**	0.18 NS	7.48*
Contingency table χ^2 value = 18.01***			
Oocytes			
Oocytes present	0 (2.03)	7 (8.78)	6 (2.19)
Oocytes not present	12 (9.97)	45 (43.2)	7 (10.81)
Column χ^2 values	2.44 NS	0.47 NS	7.97**
Contingency table χ^2 value = 10.88**			
Brooded Larvae			
Brooded larvae present	0 (0.94)	2 (4.05)	4 (1.01)
Larva not present	12 (11.06)	50 (47.95)	9 (11.99)
Column χ^2 values	1.02 NS	1.12 NS	9.60**
Contingency table χ^2 value = 11.74**			

The results of a chi-square analysis of this 2 × 3 contingency table and the results of chi-square tests for each column are indicated. Numbers in parentheses indicate the expected values for each cell. * = $P < 0.01$; ** = $P < 0.005$; *** = $P < 0.001$; NS = not significant.

nies with silhouette areas smaller than 200 mm²). After those initial losses, both age- and size-specific survivorship curves indicated a nearly constant rate of mortality, with possible increased mortality among the largest colonies.

Reproductive state

Results of chi-square analyses of the effects of colony size and colony age on reproductive state of colonies collected in May 1992 are shown in Tables II and III, respectively. For colonies of the smallest size class (<200-mm² colony-silhouette area), the frequencies of colonies bearing strobilating zooids were higher than expected; in medium-sized colonies (200–1800 mm²) the frequencies did not differ from expected values; and in large colonies (>1800 mm²) the frequencies were lower than expected. The large size class also had higher-than-expected frequencies of colonies with developing oocytes and of brooding larvae, whereas the other size classes did not differ significantly from expected values for those parameters (Table II).

Results of chi-square analyses on colony age class and reproductive state showed a significant age effect on the frequency of strobilating colonies among the youngest

age class (colonies 1 month old), but the other age classes did not differ significantly from expected values for strobilation. Age-class comparisons of the frequency of colonies bearing developing oocytes or brooded larvae did not differ from expected values (Table III). There was, however, a significant relationship between colony age and colony size (Fig. 8). Colony size appears to be a better predictor of reproductive state than colony age, but colony size is affected by colony age, because the smallest colonies tend to be young, and larger colonies tend to be older.

I used multiple regression analysis to ascertain the relative effects of colony size and colony age on oocyte size. That analysis was significant, explaining 36.87% of observed variability ($F = 21.96$; $df = 2, 75$; $P < 0.001$). Colony size accounted for 99.9% of the variability explained by the regression, whereas colony age contributed only an additional 0.01% to the explanation ($F = 0.035$ NS; $df = 1, 75$; $P > 0.75$). Colony size may thus be invoked as a primary determinant of oocyte size; colony age has a secondary effect on oocyte size because it affects colony size.

Discussion

Polyclinum planum colonies do not fragment into physiologically isolated ramets as they grow. This observation bears out the assumption made by Pearse *et al.*

Table III

Comparisons of number of colonies in each age class with zooids undergoing strobilation, bearing oocytes, and brooding larvae

	Colony age classes (months)		
	1	2-15	>15
Strobilation			
100% zooid strobilation	10 (4.85)	23 (27.38)	1 (1.76)
<100% zooid strobilation	1 (6.15)	39 (34.62)	3 (2.24)
Column χ^2 values	9.78**	1.25 NS	0.59 NS
Contingency table χ^2 value = 11.62**			
Oocytes			
Oocytes present	0 (1.85)	12 (10.47)	1 (0.68)
Oocytes not present	11 (9.15)	50 (51.53)	3 (3.32)
Contingency table χ^2 value = 3.20 NS			
Brooded larvae			
Larvae present	0 (0.86)	6 (4.83)	0 (0.31)
Larvae not present	11 (10.14)	56 (57.17)	4 (3.69)
Contingency table χ^2 value = 1.57 NS			

The results of a chi-square analysis of this 2 × 3 contingency table, and, when the contingency test is significant, the results of chi-square tests for each column are indicated. Numbers in parentheses indicate expected values for each cell. ** = $P < 0.005$; NS = nonsignificant.

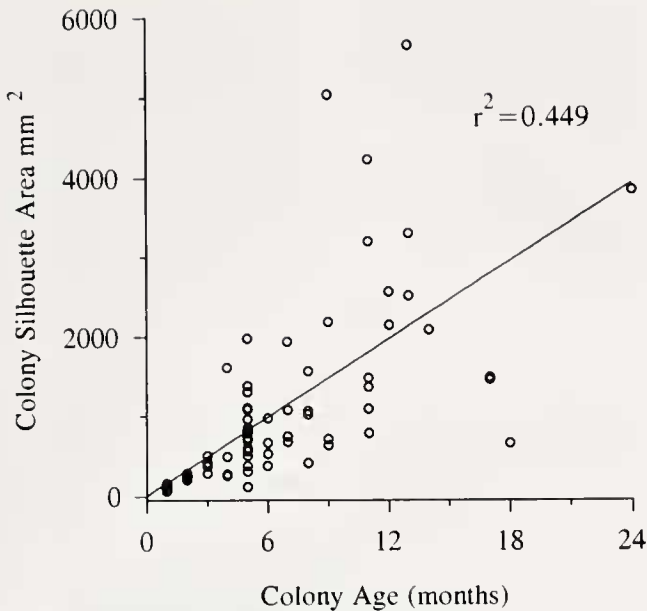


Figure 8. The relationship between colony age and colony size for *Polyclinum planum* collected in May 1992 ($n = 77$ colonies). The solid line indicates the linear regression, which was significant at $\alpha = 0.05$.

(1989) that this is a nonfragmenting species and means that each *P. planum* colony represents an entire genet. As such, the loss of a *P. planum* colony is a greater loss, in an evolutionary sense, than if it were only one of several physiologically isolated ramets. *P. planum* has consequently developed growth-related adaptations that increase the chances of colony survivorship even in physically stressful intertidal environments.

The most obvious ecological risk to erect, though flexible, intertidal colonies of *P. planum* is dislodgement by water-flow forces. Denny *et al.* (1985) demonstrated how such forces can dislodge or limit the size of intertidal organisms living in wave-impacted environments. Since intertidal *P. planum* colonies are subjected to those kinds of water flow forces, it is not surprising that this species exhibits growth-related adaptations for dealing with stresses associated with water flow. The pattern of *P. planum* colony growth reveals two strategies for mitigating the effects of water flow: (1) an attenuating pattern of growth; and (2) allometric expansion of the zooid-bearing lobe into a laterally flattened structure.

Attenuating growth, like that demonstrated by *P. planum* (see Fig. 2), is common among colony-forming modular organisms such as corals (Hughes and Connell, 1987; Karlson, 1988; Lasker, 1990), bryozoans (Hughes, 1990; Kauffman, 1981), and ascidians (Ryland *et al.*, 1984; Stoner, 1989; Stocker, 1991). In the case of *P. planum*, it appears that environmental stress limits colony size. The general pattern of *P. planum*'s attenuating growth is several months of rapid growth followed by

slowing and eventual cessation of growth. A few colonies did, however, grow continuously until they were dislodged. The typical pattern of *P. planum* growth does not differ markedly from Sebens' (1987) predictions for Indeterminate Growth Type III (Plastic Attenuating Growth), but the growth pattern of a few colonies approximated Sebens' Indeterminate Growth Type II (Plastic exponential growth).

The maximum size for a *P. planum* colony is set, at least in part, by water-flow forces. This is evidenced by the fact that some colonies, probably in protected microhabitats, produced lobes much larger than 1800 mm² (colony-silhouette area—the maximum colony size indicated by *P. planum*'s mean growth trajectory—see Fig. 2), even though susceptibility to dislodgement increased for other colonies when their silhouette areas exceeded 1800 mm² (see Table I). Similar water-flow-induced size restrictions have been suggested or demonstrated for colony-forming modular organisms such as sea fans (Birke-land, 1974) and coral (Denny *et al.* 1985), and for unitary organisms including sea urchins, limpets, mussels, and snails (Denny *et al.*, 1985).

Life-history constraints also limit colony growth. As *P. planum* colonies increase in size, they tend to become reproductively active (see Table II). The onset of reproduction is a critical event in the life history of any organism (Lloyd, 1980; Sebens, 1982; Kozłowski and Weigert, 1986). A shift from growth to reproductive activity in *P. planum* appears to occur as the rate of colony growth slows. This relationship between growth and reproduction apparently occurs not only in colonies of *P. planum* but among colonies of some other ascidians (Bak *et al.*, 1981; Brunetti *et al.*, 1988). For some clonal taxa, however, the event triggering the onset of reproductive activity can vary greatly and may include colony age, size, or environmental stimuli; in other cases neither colony age nor size is a good predictor of the onset of reproduction (Harvell and Grosberg, 1988).

Slowed growth at the onset of reproductive activity in *P. planum* is a consequence of life-history constraints on individual zooids. *P. planum* zooids are hermaphroditic, producing sperm and oocytes in gonads housed in the post-abdomen (Ritter and Forsyth, 1917). Iterative production of new zooids (*i.e.*, colony growth) involves strobilation of the post-abdomen, where gonads develop, and disorganization of the atrial chamber (Holyoak, 1992), where larvae are brooded. As a result, a *P. planum* zooid cannot simultaneously undergo strobilation and produce gametes or brood larvae.

The second growth-related strategy that *P. planum* uses to minimize the effects of water flow involves morphogenesis of the zooid-bearing lobe from a small spheroidal structure into a large laterally flattened one. Changes in the silhouette shape of marked colonies sug-

gest that *P. planum* is able to add material to just about any part of a growing lobe, thereby producing a wide range of colony shapes (see Fig. 4).

The ecological advantage of lobe flattening is evident when the morphology of *P. planum* colonies is considered in light of the acceleration of water, which, according to Denny *et al.* (1985), is the water-flow force with the greatest ability to dislodge sessile organisms. The impact of the acceleration reaction of water is directly proportional to an object's volume, not to its exposed surface area (Denny, 1993). If the spheroidal lobe of a *P. planum* recruit were to increase in size isometrically, producing a large spherical lobe, the stress from the acceleration reaction and the chance of dislodgement would hypothetically be greater for that colony than for one with a flattened lobe having the same frontal silhouette area.

Increased reproductive potential is a direct benefit of colony growth and lobe flattening. A flattened lobe has a greater surface-to-volume ratio than a spheroidal lobe. Because zooids are located only at the surface of *P. planum* colonies (Abbott, 1987), a flat lobe can house more zooids than a spheroidal lobe with the same volume. And since each zooid has the potential to produce gametes and brood larvae, the reproductive capacity of a colony is directly proportional to the number of zooids it contains. *P. planum* is therefore able to increase its surface area, maximize the number of zooids it can bear, and simultaneously minimize the effects of the water acceleration reaction by producing a flattened lobe.

One final consequence of growth is its impact on the mortality rate of recruits (Table I). Though growth beyond an environmentally imposed size limit puts the largest colonies at risk, the greatest observed mortality occurred among the smallest and youngest colonies (Fig. 7). Birkeland (1974) reported a similar trend of high mortality among smaller members of a population of sea fans growing in heavy surf. High mortality among the smallest size class of *P. planum* colonies is almost certainly a function of site selection by larvae at settlement. The long-term suitability of a site is not tested until colonies grow large enough to extend beyond the boundary layer. Only colonies with the best settlement sites and the firmest peduncular attachments will survive to grow into the larger size classes. Mortality among small colonies is almost certainly a consequence of growth because *P. planum* has no known predators, and I saw no evidence of predation on any colonies during this study.

In conclusion, colony-level growth and morphogenesis of modular organisms are large-scale effects of self-assembly processes. Those processes include the temporal and spatial iteration and arrangement of modules (Rosen, 1986; Ryland and Warner, 1986). The result of those processes is colony morphology that can convey ecological advantage (e.g., Ryland and Warner, 1986,

and references therein). Though we are learning more about the complexities and significance of modular growth, we are still largely ignorant of the mechanisms that regulate it. My data suggest that growth in *P. planum* may be regulated by a combination of external and internal factors. As we unravel the rules of colony-level modular growth, we may gain insights into the processes that regulate and drive development at other levels of biological organization.

Acknowledgments

I thank A. T. Newberry, J. S. Pearse, C. M. Young, B. Rinkevich, and two anonymous reviewers for their helpful comments on drafts of the manuscript. Support for this study was provided by the Department of Biology, University of California at Santa Cruz; Friends of the Long Marine Laboratory; the American Museum of Natural History (Lerner-Gray Fund for Marine Research); the Earl and Ethel Myers Oceanographic and Marine Biology Trust; and Manchester College.

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